PREDICTING THE DISTRIBUTION OF THICKETS AND FORESTS ON THE CAPE PENINSULA, CAPE PROVINCE USING LINEAR REGRESSION ANALYSES

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Botany honours

Ecology Project

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ABSTRACT.

Forest and thicket communities are distributed throughout fynbos. The species constituents exhibit life history characteristics significantly different from fynbos species, in that reproductive biology and recruitment are not coupled to fire. The limited occurrence of forests and thickets suggest that there may be specific abiotic factors which limit their distribution. In an attempt to determine which factors are significant in prediction, data from 600 plots covering a substantial part of the Cape Peninsula was analyzed using linear regression models. Although trends in predictive variables were detected for both forest and thickets, the models were largely unsuccessful. This was due both to the lack of inclusion or poor transformation of certain factors and the fact that not all potential forest and thicket sites are filled. The role of fire as the stochastic element in the system as well as the significance of measured environmental variables in determining forest and thicket location is discussed.

INTRODUCTION.

Fynbos is a sclerophyllous vegetation type characteristic of the Cape province of South Africa (Acocks, 1953). The vegetation is subjected to varying frequency and intensity of veld fires during different seasons throughout the year. Because of the low nutrient status of the environment, the life histories of many species, and indeed the diversity of vegetation as a whole depend on fire events. However, within the fynbos biome are isolated communities of thicket and forest species, ranging in size from extensive forests to patches a few meters in diameter. These species have different functional properties and life histories, and once established, exhibit a high degree of fire resistance and unlike fynbos, regeneration is not coupled with fire events.

The feature of fire as the major disturbance factor has been used to explain the lack of trees in fynbos (Moll et al., 1980) as high frequency of fire events may prevent forest species establishment. Forest and thicket distribution appears not only to be dependent on fire frequency but also the restrictions of shallow soils and summer drought (Campbell and Moll, 1977; van Wilgen, 1981). Forests are therefore associated with fire protected sites with deeper moister, more fertile soils (Cowling, 1984; Campbell, 1986). Thickets have similar soil associations but are mainly restricted to fire protected, drier lowland (mainly coastal) sites (Cowling and Holmes, 1992). Consequently, forest and thickets are relatively rare communities in fynbos and mainly restricted to kloofs, steep slopes with a southerly aspect, riverine valleys or coastal sites. It has been suggested that successful establishment of these communities appears to be dependent, not only on site characteristics but also mechanisms of dispersal and regeneration (Manders, 1991).

The evidence from studies suggest that forest and thicket could potentially occupy many more sites than they do presently. Unlike most species in fynbos, one characteristic feature of some forest and thicket species is that the seeds are bird or wind dispersed fruits whose recruitment is not coupled to fire events (Manders, 1992). While the mechanisms of dispersal (eg. by birds) resulting in preference for certain sites (eg. suitable perches), or amenochocory resulting in decreasing density away from forest or thicket edges, it can be surmised that over time there would be a reasonable spread of propagules into fynbos. It is apparent therefore, given the existing distribution of forest and thicket communities, that other site characteristics or events determine successful establishment. It is proposed that site characteristics such as soil type, relative intensities of solar radiation (dependent on aspect and angle of slope), soil moisture content (especially during the summer period) and exposure to fire are of primary importance in the establishment phase and maintenance of forest and thicket communities.

That these forest and thicket communities occur infrequently in small patches, makes them vulnerable to disturbance. This gives them a high conservation priority throughout the floristic region. This is especially true for the Cape Peninsula, where due to high population of the area, there are intense developmental pressures on the environment. For this reason development of an explanatory predictive model for these community patterns would assist in environmental management of the area. Although there has been a number of studies of a number of areas and communities on the Cape Peninsula (eg. Campbell and Moll, 1977; Glyphis et al., 1978; Laidler et al., 1978; McKensie et al., 1977; Taylor, 1969), these have largely focused on either single communities eg. forests or, with the exception of the study by Taylor (1969) single areas with their related plant communities. Therefore not only are there large unsurveyed areas, but also there has not been a comprehensive collation of all communities on the Peninsula. In order to calculate predictive models for community distribution, an extensive data base is needed, covering a covering the range of environmental and biotic variation.

This project intends to highlight the environmental factors which are precursors to forest and thicket establishment and maintenance, through the use of linear regression analysis. Thus it is the aim of this project to test and develop hypotheses regarding the distribution of forest and thicket plant communities. Two questions are posed:

1. What are the key abiotic factors which determine colonisation and location of forest and thicket species in the Cape Peninsula?

2. Do mathematical models such as multiple regression and stepwise regression represent a successful method of predicting the location of vegetation communities?

The application of regression models to ecological systems.

Management of biological systems requires considerable knowledge of the many aspects of ecological mechanisms in operation. It is impossible to evaluate the importance of every aspect of all the ecological variables. However, it may be possible given local knowledge or access to data over time, to estimate those parameters which are of the greatest importance in dictating patterns in the environment. Interpretation of field data is essential in order to produce some working management policy for any one area. However, this information, if taken at one instance in time, may not reflect the dynamics of the system, and therefore it is difficult to produce predictive conclusions. The production of predictive mathematical models from such data have been traditionally been produced form simple regression models.

A standard linear regression relates one independent variable to an independent variable. The standard linear regression model is given by equation 1.

$$Y_i=a+b.x_i+e_i$$

[1

where Y^i is the observed response, x_i the predictor variable, a and b parameters describing the relationship between y_i and x_i and e_i (error or residual) the difference between the prediction given by $a+b.x_i$, ie. a random (or unpredicted) component.

This assumes that given multiple observations of the predictor variable x_i will be independent and normally distributed. Simple presence/absence counts are normally considered to be distributed binomially, whereas frequency of occurrences would follow a Poisson distribution. As many ecological data sets have these different types of distributions, the linear form of the equation can be maintained as the expectation is equal to the systematic part of the model, and that there is therefore a linear relationship between the systematic and predictive components of the equation (Nicholls, 1990). The general format of the multiple regression model is given by equation 2:

$$y=a+b_1.x_1+b_2.x_2+...+b_k.x_k$$

[2

where the response variable y is directly related to a series of parameters (b) and variables (x). This creates a regression or response surface in multidimensional space.

The assumptions of the linear regression model are threefold:

1. The errors are normally distributed.
2. The mean of the error terms is zero.
3. The error terms have a constant variance for all combined values of the independent variables.

(Groebner and Shannon, 1989)

The model is thus created by mathematically determining which of the variables most significantly influence the response. Given a relationship between the predictor and response, a frequency distribution can be assumed and variables in turn fitted to the model. This is achieved by forward stepwise selection, whereby each variable that presents the greatest significant change in the deviance is retained in the model. This procedure is repeated until either there are no more variables, or remaining variables do not significantly change the deviance. In creating a model Nicholls (1990) suggests there are three critical interactive stages:

1. The selection of an appropriate statistical model.
2. The selection of suitable site variables to be used as predictors.
3. Critical evaluation of fitted regression model for outliers.

Creation of a suitable predictive model is an interactive process whereby initial guesses are continually tested and if necessary, modified. It is apparent therefore that some degree of testing of the distribution of the data be carried out prior to the final fitting of the model.

METHODS.

Study site.

Data for this study was collected from both past published and unpublished studies and direct field measurement. The studies focused either on specific plant communities or one particular area on the Cape Peninsula. The study sites were selected from the area of the Cape Peninsula from Signal Hill (Latitude 33° 55' S, Longitude 18° 24' E), southward to the northern boundary of the Cape of Good Hope Reserve (latitude 34° 14' S longitude 18° 27' E).

The geology consists of coarse grained granite overlain by Table Mountain sandstone and to a lesser extent by Malmsbury shales on Signal Hill on the northern limit of the study area. The granite is exposed in many areas on the lower slopes of the mountains, particularly on the steeper coastal slopes.

The soils mainly reflect the underlying substrata. Mountain areas are dominated by shallow leached coarse sands (Mispahs) containing a varying proportion of organic matter. Soils on mountain slopes, depending on deposition conditions, vary from colluvial soils (eg. Hutton or Clovelly forms), litholic (Glenrosa) forms or granite derived soils. Forested areas such as in kloofs have associated deep colluvial black soils (Oakleaf form). On many slopes and valleys the has been considerable build up of coarse sandstone derived deposits. In coastal areas this alternates with deep, calcareous, aeolian, finer grained, calcareous sands.

The area receives considerable local variation in rainfall, largely associated with influence of orographic effects. Mean annual rainfall ranges from 600 mm in the south to over 2400 on table mountain. Mountain summits above 500 m often experience mists throughout the year associated with approach of cold fronts. Climate is of the mediterranean type with temperatures ranging from 5°C - 20°C in winter, to 14°C - 30°C in summer. There is considerable variation in solar radiation on slopes where radiation on a steep north slope in winter (lower azimuth) is considerable higher than a southerly slope. In summer, although there are generally higher levels of incoming solar radiation the difference with respect to slope aspect and angle is greatly reduced.

All recorded site information conformed to Braun-Blanquet concepts and techniques (Werger, 1974) of estimating vegetation cover and edaphic site variables. Data from 598 plots were adjusted into a standardised format and entered into spreadsheet format for analysis. For the purpose of this study, in addition to plant species number and percentage cover, eight site variables were measured and extracted from the database (Table 1).

Table 1. Units and abbreviations of measured site variables.

Variable	Units	Abbreviation
Distance from coast	kilometres	DIS
Altitude	meters	ALT
Aspect rank	rank	ASP
Slope	degrees	SLO
Soil depth	centimetres	SDE
Rainfall	mm x100	RAI
Radiation load	$10^6 Jm^{-2}day^{-1}$	RAD
Rock cover	%	RCO

Variables, such as species cover, rock cover etc., could be extracted directly. However, soil data collated from both field sampling, soil maps and knowledge of the sites, were qualitatively ranked according to the South African binomial classification system, (table 2)(MacVicar et al.,1977).

Table 2. Soil type category allocation.

Category	Soil description
1	Shallow sand on Table Mountain Group sandstone. (ie. Mispah)
2	Red to yellow colluvium (ie. Hutton)
3	Red to yellow soil on granite
4	Quaternary calcareous dune sand (ie. Fernwood)
5	Tertiary yellow sand
6	Sandy loam on shale
7	Deep colluvium (ie. Oakleaf)

Utilising a series of tables relating slope angle and aspect to solar azimuth, values for aspect and slope were integrated using Schulze's (1975) radiation model, which expressed a value for incoming solar radiation fluxes. For the purpose of this exercise the equinox values were taken as compromise indications of solar load throughout the year. In addition, an alternative, simple qualitative ranking system was calculated relating aspect alone with solar input (after Campbell, 1985). This simply relates aspect to a radiation index whereby more northerly and secondarily westerly radials have a higher solar input than southerly and easterly radials.

Mean annual rainfall values were interpolated from isohyets on 1:250 000 rainfall map of Cape Town. Plant species were sorted into three groups (see Appendix I for species lists):

1. Pure forest species.
2. Pure thicket species.
3. Species occurring in both forest and thicket not including groups 1. and 2.

For analysis of each formation, pure forest (1) and pure thicket (2) species were sorted and combined with those species occurring in both (3).

Variables were tested both for correlations against each other and for linearity against forest and thicket data. For both forest and thicket species the relationships were analyzed using multiple and stepwise regression. Having tested for significance, only those variables which had $p < 0.05$ were entered into the multiple regression. Addition of these redundant variables decreased the strength of the model and so were rejected. For stepwise variable selection an only variables with an F-ration of greater than 4 were selected. The significance of R^2 values was tested with an F-test. Soil categories were tested for independence with respect to forest and thicket communities using Chi-squared test. Generalised Linear Modelling (GLIM) analysis was also attempted however due to the failure of the software to accept both factorial data and the import presence-absence species data the programme was rejected.

RESULTS.

The correlation matrix (table 3) indicates the degree to which site variables may be related with each other. This allows some adjustment to models where any cyclic interaction between variables may be allowed for. This may be a natural property of related environmental variables, for example, rainfall with altitude or distance form coast, or attribute of the mathematical calculation for example, computed radiation load and aspect. Direct regression analyses of site variables with plant species cover, for forest and thicket species (table 4), as a test of linearity, cover revealed few strongly significant relationships. Considerable

Table 3. Correlation matrix (Pearsons r values) for site environmental variables.

	DIS	ALT	SLO	RAD	SDE	RAI	RCO
ASP	0.33 ***	0.06 ns	0.04 ns	0.58 ***	0.05 ns	0.22***	0.8 ns
DIS		0.32 ***	0.12 **	0.14 ***	0.22 ***	0.51 ***	0.22 ***
ALT			0.05 ns	0.3 ns	0.26 ***	0.52 ***	0.16 ***
SLO				0.52 ***	0.17 ***	0.7 ns	0.19 ***
RAD					0.5 ns	0.18 ***	0.9 *
SDE						0.15 ***	0.43 ***
RAI							0.14 ***

Table 4. Correlation coefficients for site environmental variables against species cover for forest and thickets. n = 598 *** = p<.001, ** = p < 0.01, * = p < 0.05..

	Forest and thicket	Forest	Thicket
DIS	+0.344***	-0.343***	-0.30ns
ALT	-0.263***	-0.158***	-0.321***
ASP	+0.300***	+0.388***	+0.213***
SLO	-0.184ns	-0.070ns	-0.274*
RAD	+0.486***	+0.206***	+0.361*
SDE	+0.077ns	-0.069ns	+0.006ns
ISO	+0.3376*	+0.260***	-0.170ns
RCO	+0.0316ns	+0.0519ns	-0.0054ns

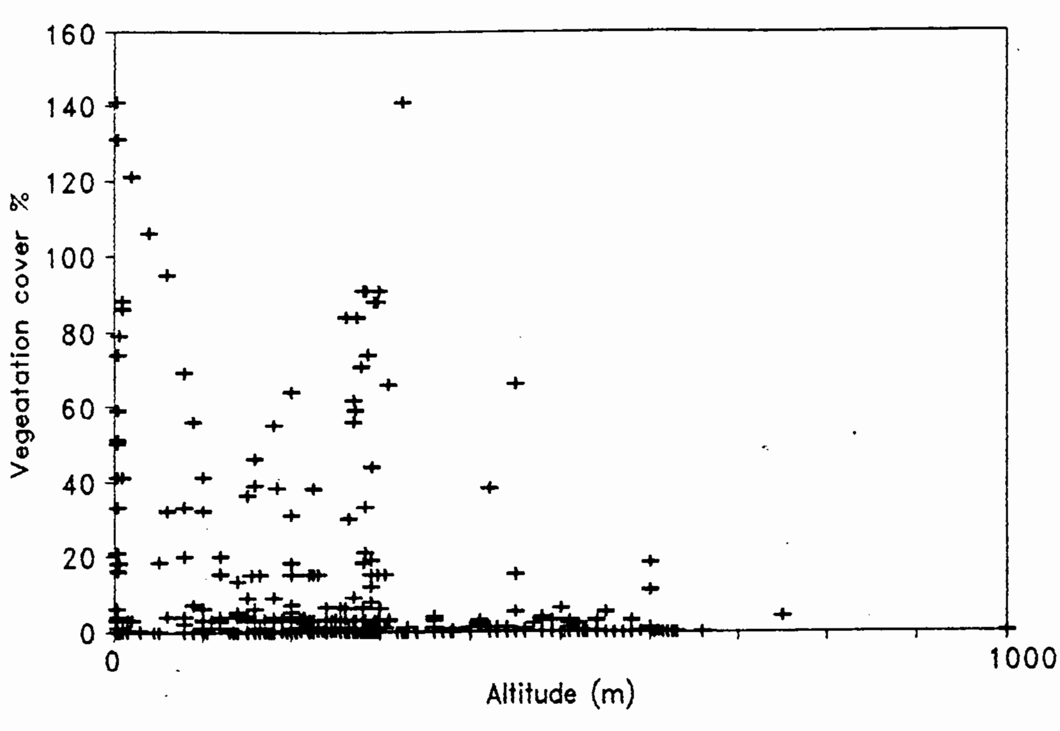

Figure 1. Scatter diagram showing the relationship between thicket cover with altitude. $R^2 = 0.103$ $p < 0.001$.

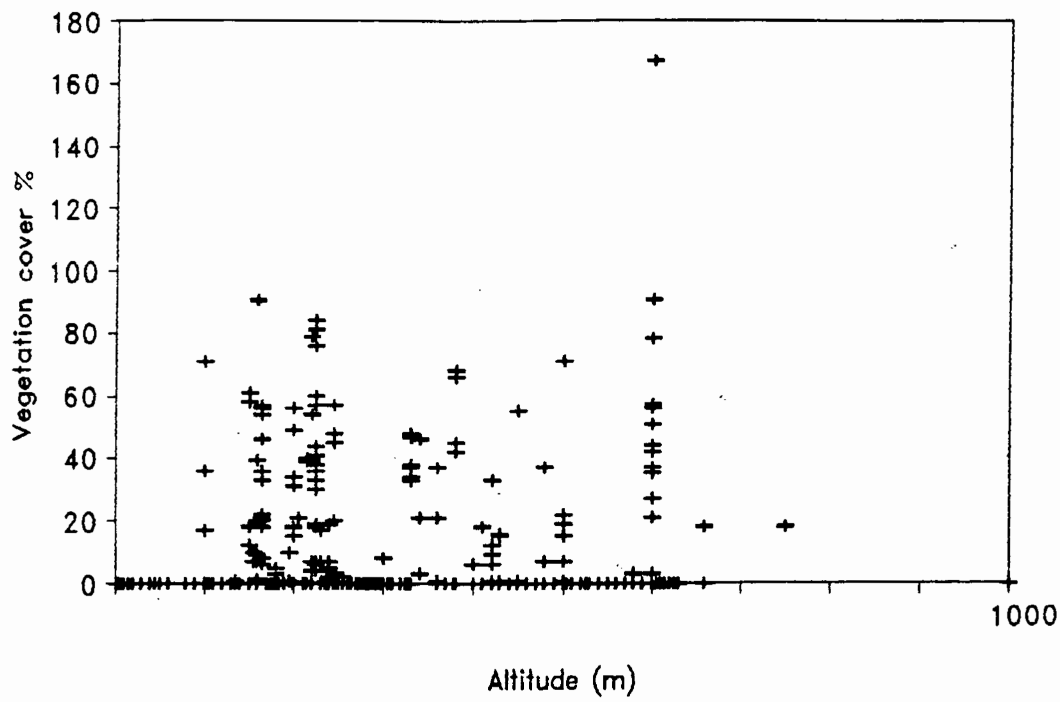

Figure 2. Scatter diagram showing the relationship between forest cover with altitude. $R^2 = 0.025$ $p < 0.001$.

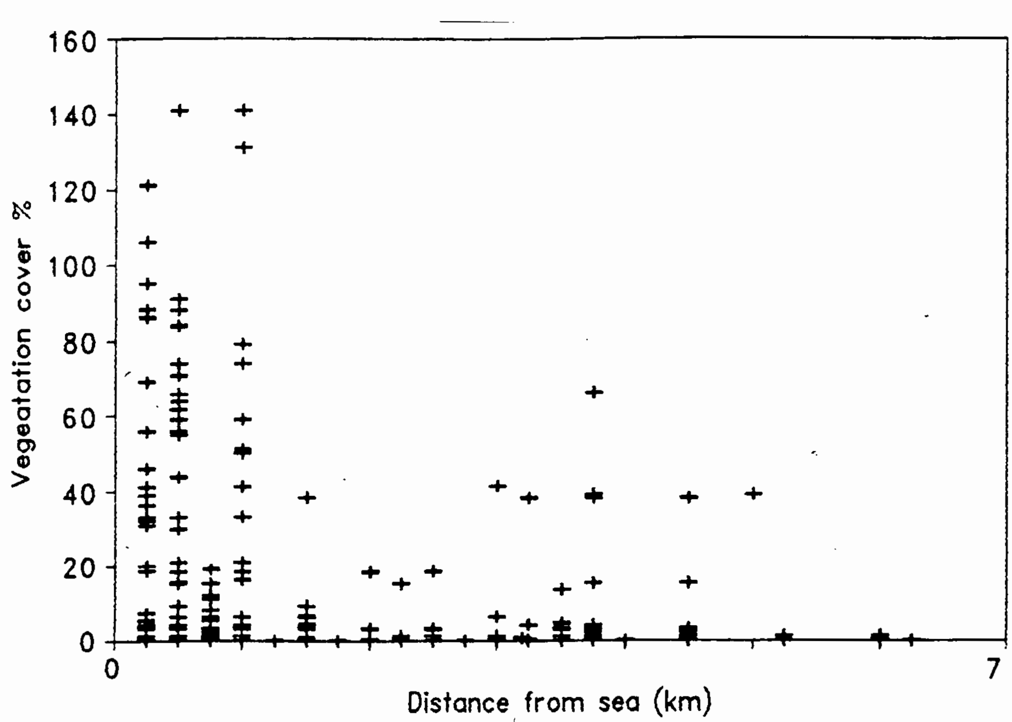

Figure 3. Scatter diagram showing the relationship between thicket cover with distance from sea. $R^2 = 0.09$ p ns.

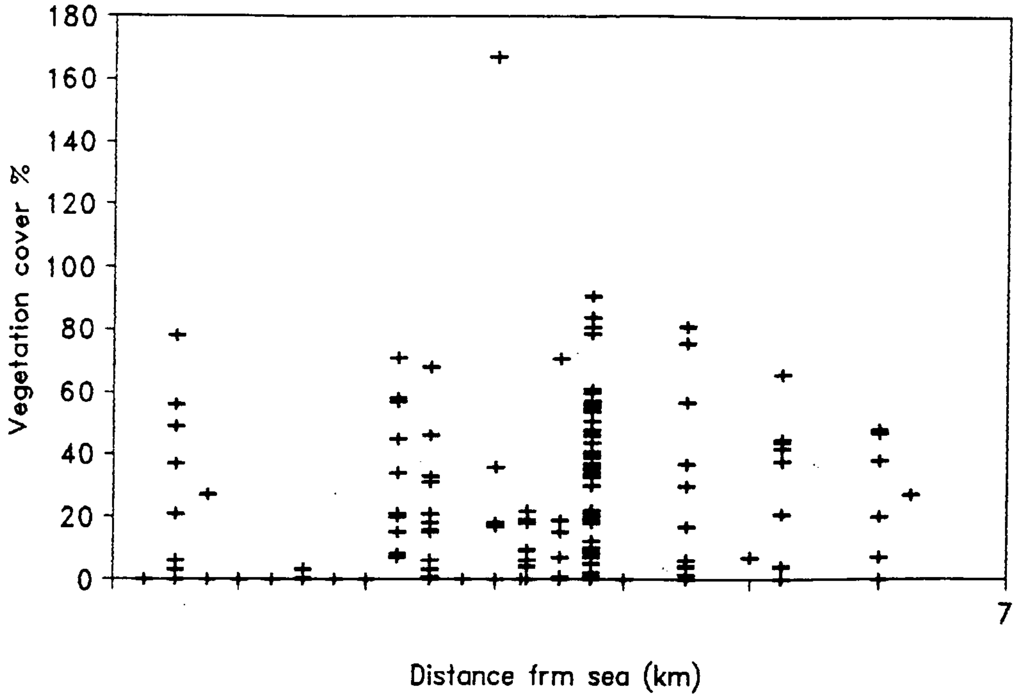

Figure 4. Scatter diagram showing the relationship between forest cover with distance from sea. $R^2 = 0.119$ $p < 0.001$.

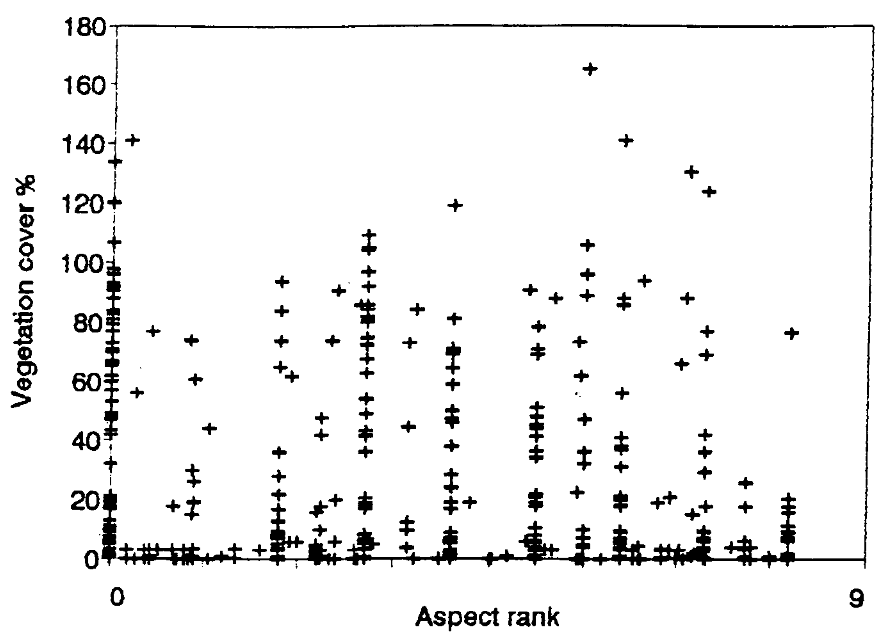

Figure 5. Scatter diagram showing the relationship between thicket cover with aspect rank. $R^2 = 0.045$ $p < 0.001$.

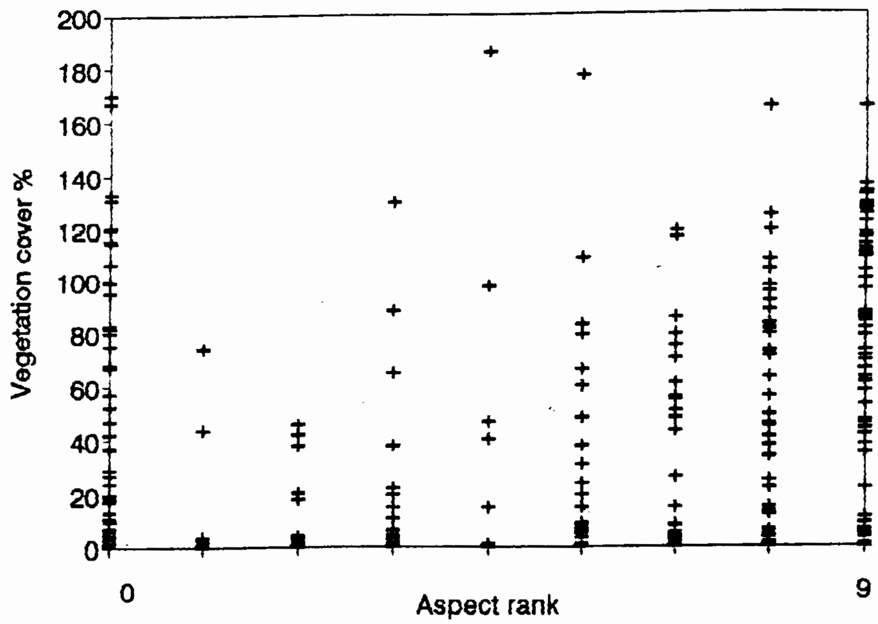

Figure 6. Scatter diagram showing the relationship between forest cover with aspect rank. $R^2 = 0.152$ $p < 0.001$.

scattering of data points (figures 1 - 6) even failed to conform to a linear relationship even when transformed. Examination of these scatter plots shows that there is generally an increase in frequency toward zero percentage cover. This tends to create enough noise on the graph to corrupt any significant linearity. However, the indicated trends (eg. forest with aspect rank and distance from sea, thicket with altitude) are further highlighted in the mathematical models below.

As the regression values were somewhat lower than expected additional regression analyses were run on forest and thicket plots with null data sets, that is containing only those plots with forest or thicket species. The data therefore represent sites where forest or thicket species are established within other fynbos communities, but not necessarily true forest or thicket communities (ie. those tending toward 100% cover of community species).

Multiple regression analysis (table 5) showed low R^2 values but with certain significant factors which varied to some extent according to the two communities. From this data model fitting coefficients for forest and thicket communities were computed (tables 6 and 7). Similarly stepwise regression analysis was conducted for the data set revealing marginal differences in significant variables (tables 8,9 and 10). All regression values (F-tested) significantly ($p < 0.01$) explained the calculated proportion of variation in model. Even though the calculated variation was small in most cases, multiple regression and stepwise regression models were calculated for both forest and thicket data sets.

Table 5. Regression analyses for site environment values against species cover of forest and thicket with null vales removed.

	Forest	Thicket
DIS	+0.404 ***	+0.08 ns
ALT	-0.26 ns	-0.28 ***
ASP	+0.457 ***	+0.225 ***
SLO	-0.26 ***	-0.28 ***
RAD	-0.023 ns	-0.022 ns
SDE	-0.014 ns	+0.036 ns
RAI	+0.38	+0.01 ns
RCO	+0.038 ns	-0.0004 ns

Table 6. Significance values for correlation coefficients of variables as calculated by multiple regression analysis for forest and thicket species. *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$.

	Forest and thicket	Forest	Thicket	Forest plots only	Thicket plots only
DIS	**	***	NS	***	NS
ALT	***	***	***	NS	***
ASP	***	***	***	***	***
SLO	NS	NS	NS	***	***
RAD	NS	NS	NS	NS	NS
SDE	NS	NS	NS	NS	NS
RAI	NS	**	NS	***	NS
RCO	NS	NS	NS	NS	NS
R^2	0.160	0.193	0.140	0.410	0.164

Table 7. Coefficients fitted to multiple regression model for forests. *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$. F value refers to significance of R^2.

	Forest with null plots			Forest without null plots		
Factor	coeff.	p <	std. error	coeff.	p <	std. error
Constant	-20.59	***	4.43	-70.49	*	25.47
DIS	4.35	***	1.02	6.25	***	1.45
ALT	-0.04	***	0.01	-0.08	***	0.02
ASP	4.59	***	0.60	7.27	***	1.41
ISO				4.78	***	0.83
R^2	0.193 *** F=28.8 p < 0.01			0.41 *** F=24.7 p < 0.01		

Table 8. Coefficients fitted to multiple regression model for thickets. *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$. F value refers to significance of R^2 .

	Thicket with null plots			Thickets without null plots		
Factor	coeff.	p <	std. error	coeff.	p <	std. error
Constant	18.86	***	3.18	32.49	***	4.69
ALT	-0.04	***	0.87	-0.05	***	0.01
ASP	2.19	***	0.01	3.14	***	0.73
SLO				-0.39	***	0.11
R^2	0.140 *** F= 28.8 p < 0.01			0.164 *** F=20.59 p < 0.01		

Table 9. Significance values of correlation coefficients for environmental variables as calculated by stepwise regression analysis for forest and thicket species. *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$.

	Forest and Thicket	Forest	Thicket	Forest plots only	Thicket plots only
DIS	NS	***	NS	**	NS
ALT	***	***	***	***	***
ASP	***	***	***	***	***
SLO	NS	NS	NS	***	***
RAD	NS	NS	NS	NS	NS
SDE	NS	NS	NS	NS	NS
RAI	NS	NS	NS	***	NS
RCO	NS	NS	NS	***	NS
R^2	0.113	0.184	0.120	0.410	0.164

Table 10. Variable coefficients fitted to stepwise regression model for forest species. Cut off variable selection at F-ratio = 4. *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$. F value refers to significance of R^2.

	Forest with null plots			Forest without null plots		
Factor	coeff	p <	std. error	coeff.	p <	std. error
Constant	-5.91	*	3.20	-26.25	**	7.94
DIS	5.28	***	5.88	6.15	***	1.41
ALT	-0.02	***	0.01	-0.07	***	0.02
ASP	3.42	***	0.54	5.26	***	0.91
SLO				-0.61	***	0.15
ISO				4.48	***	0.81
RCO				0.24	***	0.09
R^2	0.18 *** F=58.4 p < 0.01			0.41 *** F=26.89 p < 0.01		

Table 11. Variable coefficients fitted to stepwise regression model of thicket species. Cut off selection at f-ratio=4. *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$. F value refers to significance of R^2.

	Thicket with null plots			Thicket without null plots		
Factor	coeff.	p <	std. error	coeff.	p <	std. error
Constant	19.08	***	3.05	32.49	***	4.69
ALT	-0.03	***	0.00	-0.05	***	0.011
ASP	1.82	***	0.48	3.14	***	0.73
SLO				-0.39	***	0.12
R^2	0.12 *** F=45.77 p < 0.01			0.16 *** F=20.59 p < 0.01		

The final models were:

Multiple regression model for forest

$$Cov_{forest} = 4.35DIS - 0.04ALT + 4.59ASP - 20.59 \quad [3$$

$$Cov_{forest*} = 6.25DIS - 0.08ALT + 7.27ASP + 4.78ISO - 70.49 \quad [4$$

Stepwise regression model for forest:

$$Cov_{forest} = 5.28DIS - 0.02ALT + 3.42ASP - 5.91 \quad [5$$

$$Cov_{forest*} = 6.15DISt - 0.07ALT + 5.26ASP - 0.61SLO + 4.48RAI - [6$$

$$0.24RCO - 26.25$$

Multiple regression model for thicket:

$$Cov_{thicket} = 2.19ASP - 0.04ALT + 18.86 \quad [7$$

$$Cov_{thicket*} = 3.14ASP - 0.05ALT - 0.39SLP + 32.49 \quad [8$$

Stepwise regression model for thicket:

$$Cov_{thicket} = 1.82ASP - 0.03ALT + 19.08 \quad [9$$

$$Cov_{thicket*} = 3.14ASP - 0.05ALT - 0.39SLO + 32.49 \quad [10$$

where Cov = % cover for forest of thicket (asterisk signifies model derived from data set excluding null plots), DIS = distance from sea (km), ALT = altitude (m), ASP = aspect rank, SLO = slope (degrees) RAI = rainfall (mm x 100), RCO = rock (% cover)

To test the most effective model (stepwise regression for forest species), a random sample of 200 plots was taken from the database, and expected vegetation cover calculated. This gave an R^2 value of 0.13, which approximates to the calculated estimation of explanation of variance ($R^2 = 0.18$) of the model.

Soil type information was arranged into qualitative categories and therefore was not included into regression models. Unfortunately these data were also not able to be included into the GLIM programme due to a fault in the software. Therefore the influence of soil type on plant community was assessed independently using a contingency table and Chi-squared test (table 12). This shows a strong relationship between fynbos on Mispah soils, thicket species on black colluvial and calcareous sands, and forest on black colluvial soils.

Table 12. Contingency table for vegetation type and soil type. Numbers indicate counts of plots with greater than 50% cover for forest and thicket and greater than 99% cover for fynbos. Percentage counts in brackets. $\chi^2 = 297.5$ df = 12 $p < 0.00001$. Soil types 1 = white to black (organic) sand, Table Mountain Sandstone derived (eg. Mispah), 2 = red to yellow colluvium (eg. Hutton), 3 = red to yellow clay soil, granite derived, 4 = white calcareous sand, 5 = older leached yellow sands, 6 = sand and clay soil, shale derived, 7 = deep colluvial organic soil (eg. Oakleaf).

Vegetation	Soil Type						
	1	2	3	4	5	6	7
Forest	0(0)	9(9)	16(16)	1(1)	0(0)	1(1)	72(72)
Thicket	3(3)	10(12)	11(13)	23(28)	2(2)	2(2)	32(38)
Fynbos	163(60)	52(19)	2(1)	23(8)	1(1)	10(4)	21(8)

DISCUSSION.

Given the measured variables, these models do not adequately predict the distribution of either forest or thicket species. Analysis of the scatter plots (figures 1-6) with table 3 demonstrates that the regressions are essentially non linear and data transformation is necessary. They do indicate however, the relative importance of those variables which are most likely able to predict distribution. Those are:

Forest communities.

1. Distance from Sea.
2. Altitude.
3. Aspect rank (indication of solar load).
4. Slope.
5. Isohyet (rainfall).
6. Rock cover.

Thicket communities.

1. Altitude.
2. Distance from sea.
3. Aspect rank.
4. Slope.

It can be seen that many of these variables are not mutually independent (table 3), for example altitude and distance from sea. However given these relationships between variables, if the model is improved by inclusion of both, than other hidden properties may be revealed.

For example, the relationship between distance from sea and altitude may reveal temperature gradient, susceptibility to fog or mist or reflect reproductive biology (bird dispersal range).

It can be implied from these models that forest communities are more likely to be found in inland sites, at low altitude on southerly facing slopes in higher rainfall areas with increasing rock cover. There are fewer reliable, predictive variables for thicket distribution. The indications are however that thickets are located at low altitude, close to the coast, preferring more southerly facing, lower gradient slopes. The model also exposes other factors, for instance, although thickets are normally associated with coastal areas, the correlation with altitude is stronger, ie. they are also found at low altitude (ie. in valleys) on the peninsula.

It would seem however, that there are many potential sites for thickets (valleys or coastal sites) and forests (inland, southerly facing slopes), that are not filled by these formations. The models are therefore excluding important variables or there is additional stochastic element.

Knowledge of fynbos ecology suggests that this random input is provided by fire. Even if forest or thicket species establish, high fire frequency will at the least reduce reproductive capacity of resprouters or at worst destroy individuals. It would be essential therefore to include a quantitative assessment of proneness to fire in an improved model.

The strong soil-type - community correlation (table 12) also suggests that a factor representing substrate, also needs to be included in the model, for example as a fertility rank. Care has to taken in interpretation of the relationship between soil type and vegetation, as there is a degree of circularity of causality, in that plant communities may modify soil. Given sufficient time the original soil type during establishment phase will be either altered or buried by progressive build up and decomposition of organic matter. Existing evidence shows that throughout the fynbos biome, thicket and forests (Cowling 1984) are found on soils with higher nutrient status. The phenomenon that forests exist on higher nutrient soils than surrounding fynbos has been supported by evidence by Campbell (1986). It has been shown that on Table Mountain quartzites, which predominate on the Cape Peninsula, both forest and thicket soils have a significantly higher clay and silt content, S-value, oxidizable carbon, total nitrogen and available phosphorous than surrounding fynbos soils (Cowling, 1984). However van Daalen (1981) and Knight (1988) have suggested that afromontane forests may develop on identical soils, which indicates that increased fertility may be a consequence of the nature of nutrient cycling associated with forest systems (Cowling and Holmes, 1992).

While the process of forest development is more rapid where both soil moisture and nutrient levels are higher (Campbell, 1985), the importance of this elevated nutrient level in relation to establishment is open to question. Studies by Manders (1992), on the establishment of forest species showed that while there was no limitation to germination according to soil type, the establishment of forest species was dependent on other ameliorating factors such as litter and shade which alter site microclimate and soil moisture status. 40% of forest species, as opposed to 10% of fynbos species are dispersed by vertebrates, mainly birds and therefore distributed in higher densities under suitable perch sites eg. emergent shrubs in fynbos or even rocky outcrops. These ameliorated conditions under perch sites may well have a positive influence on seedling establishment. Alternatively anemocochorous seeds, are deposited uniformly in decreasing density away from source. Although bird and wind dispersal distances are limited, the frequency of location forest and thicket communities as seed sources across the peninsula, given its dimensions, would lead to a fairly even spread of propagules, certainly encompassing many potential occupiable sites. This naturally raises further questions regarding the limitations of site to forest and thicket establishment.

Manders (1991) indicates that in formation of nuclei some forest species are colonisers into fynbos (eg. *Olea europaea ssp. africana*, *Kiggelaria africana*), while others with a ability to survive fire act as persisters (eg. *Maytenus oleoides, Olinea ventosa*). So although forest and thickets may have fire sensitive elements (eg. *Podocarpus spp.*), once established, these formations are largely fire resistant (Manders 1990). The growth period/critical size needed to attain this requires examination. It seems likely therefore that as these communities are not coupled with fire events other factors determine establishment for example, the importance of the regeneration niche (Grubb 1977) and establishment of forest and thicket nuclei.

Given the exclusion of fire during the recruitment stage White (1978) proposes that the establishment of forest species is dependent on water availability particularly during the summer. Thus seedlings growing in high temperatures, such as on slopes with a northerly aspect are less likely to survive both the high summer temperatures, water deficit and the increased possibility of fire. Manders (1992) demonstrated that establishment of forest species is not dependent on high soil moisture alone, and that increased litter, shade and high quality soil achieved maximum establishment. This conforms to Campbell's (1985) prediction that successful forest and thicket species establishment occurs between fires, only where soil moisture and nutrient levels are higher. Thus normally, forest and thicket species are essentially transient species in fynbos eliminated by fire and any condition that reduces the likelihood of fire will promote formation development and ultimate fire resistance.

It is apparent that in order to calculate a more adequate model for prediction of these community distributions there should be additional parameters included, and more suitable manipulation of existing site variables. Further addition of sampled sites set would also institute a more representative data set and assist avoid any bias towards specific community types presently in the data base. It is likely that soil data, which was left out of these models would have a significant effect on predictive power needs to be included. Data on the soil would need to be deduced from field sampling (eg. pH and CEC) or as a less accurately from existing soil maps. Soil types can be ranked qualitatively or quantitatively (according to a fertility gradient) and entered into the model. In addition information concerning fire history and vulnerability would be vital. Probability of occurrence of fire events is dependent on several variables such as existing necromass and distance to a natural barrier, such as the coast. A fire resistant zone can also be caused by any poorly vegetated surface such as a scarp or scree. Therefore site position and/or description with respect to these variables would be beneficial. Proneness to fire cold also be deduced indirectly from the existing records of fire history of the area (ie. frequency of burn over time and time since last event), and plant community type.

The measure of radiation load which has been indicated in these results from both continuous calculation (after Schulze, 1975) and ranked data (after Campbell, 1985) as being somewhat important also needs increased precision. It is suggested that the use of the programme "Radslope" (Schulze, 1988) would aid this.

This study indicates that linear modelling is a powerful predictive tool once appropriate predictive variables are entered. Modelling accents those data which are the better predictors and similarly indicates the need for additional factors to be included. Standard regression models could be improved by removal of outliers. However, it is suggested that given such a large data set it is unlikely that the few existing outlier points would contribute greatly the final models. Additionally to overcome the problem of discrimination between communities and their relation to environmental variables detrended correspondence analysis would augment the prediction models.These additional techniques remain to be tested.

CONCLUSIONS

The success of colonisation of forest and thicket species in fynbos appears to be primarily a result of the fact that seed dispersal and establishment is not coupled to fire events and secondarily environmental conditions during seedling phase. The question of whether or not certain factors, such as soil nutrient levels, influence seedling success remains. It is debatable to what extent soil water status is critical during seedling establishment, and this in turn is dependent on slope and aspect of site. While the distinction of those environmental factors which influence the location forest and thicket communities is recognised, the degree of variance associated with any direct linear relationship with one or several factors, indicates that there is one or more additional parameters not examined here. The models indicate that predictability of community location is difficult because of a stochastic element. Knowledge of fynbos suggests that this variation is associated with either fire alone or this together with a degree of stochasticity due to other factors. History of a site is therefore a primary factor in determining location of plant communities. The observation that there are many apparent potential sites for either thicket (along coasts) or forests (in many kloofs and valleys) suggests that these fynbos sites presently, although not necessarily always, exhibit a susceptibility to fire. Thus this information can be used to predict in which locations forest or thicket is likely to establish given the exclusion of fire. What is not clear from this study is which variables predict fire proneness. It can be speculated that such variables as proximity to sea or water course, proximity to cliff face, high percentage rock cover etc. would result in a decreased fire risk, and a quantitative measure of this would be essential for future models. Once the relative importance of the effect of fire on forest and thickets can be assessed through modelling then the extent to which forest and thickets would invade fynbos could be more accurately predicted.

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Appendix 1. Species associated with forest only, thicket only and both.

Forest species.

Celtis africana

Diospyros whyteana

Halleria lucida

Hartogiella schinoides

Ilex mitis

Kiggelaria africana

Ocotea bullata

Olea capensis subsp. macrocarpa

Olinia ventosa

Podocarpus falcatus

Podocarpus latifolius

Prunus africana

Pterocelastrus rostratus

Rapanea melanophloeos

Scolopia mundii

Thicket species.

Cassine maritima

Chrysanthemoides monelifera

Chironia baccifera

Colpoon compressum

Cussonia thrysiflora

Diospyros glabra

Dodonaea viscosa

Euclea acutifolia

Euclea racemosa

Euclea tomentosa

Maurocenia frangularia

Myrica cordifolia

Myrica serrata

Olea exasperata

Protasparagus capensis

Protasparagus compactus

Protasparagus exuvialis

Protasparagus retrofractus

Protasparagus rubicundis

Protasparagus stipulaceus

Putterlickia pyracantha

Rhus crenata

Rhus glauca

Rhus laevigata

Sideroxylon inerme

Tarchonanthus camphoratus

Species occurring in both forest and thicket.

Brabejum stellatifolium

Brachylaena neriifolia

Cassine peragua

Grewia occidentalis

Maytenus acuminata

Maytenus heterophylla

Maytenus oleoides

Meterosideros angustifolia

Myrsine africana

Myrsine pillansii

Olea capnsis subsp. capensis

Olea europaea

Protasparagus aethiopicus

Protasparagus africanus

Pterocelastrus tricuspidatus

Rhus angustifolia

Rhus lucida

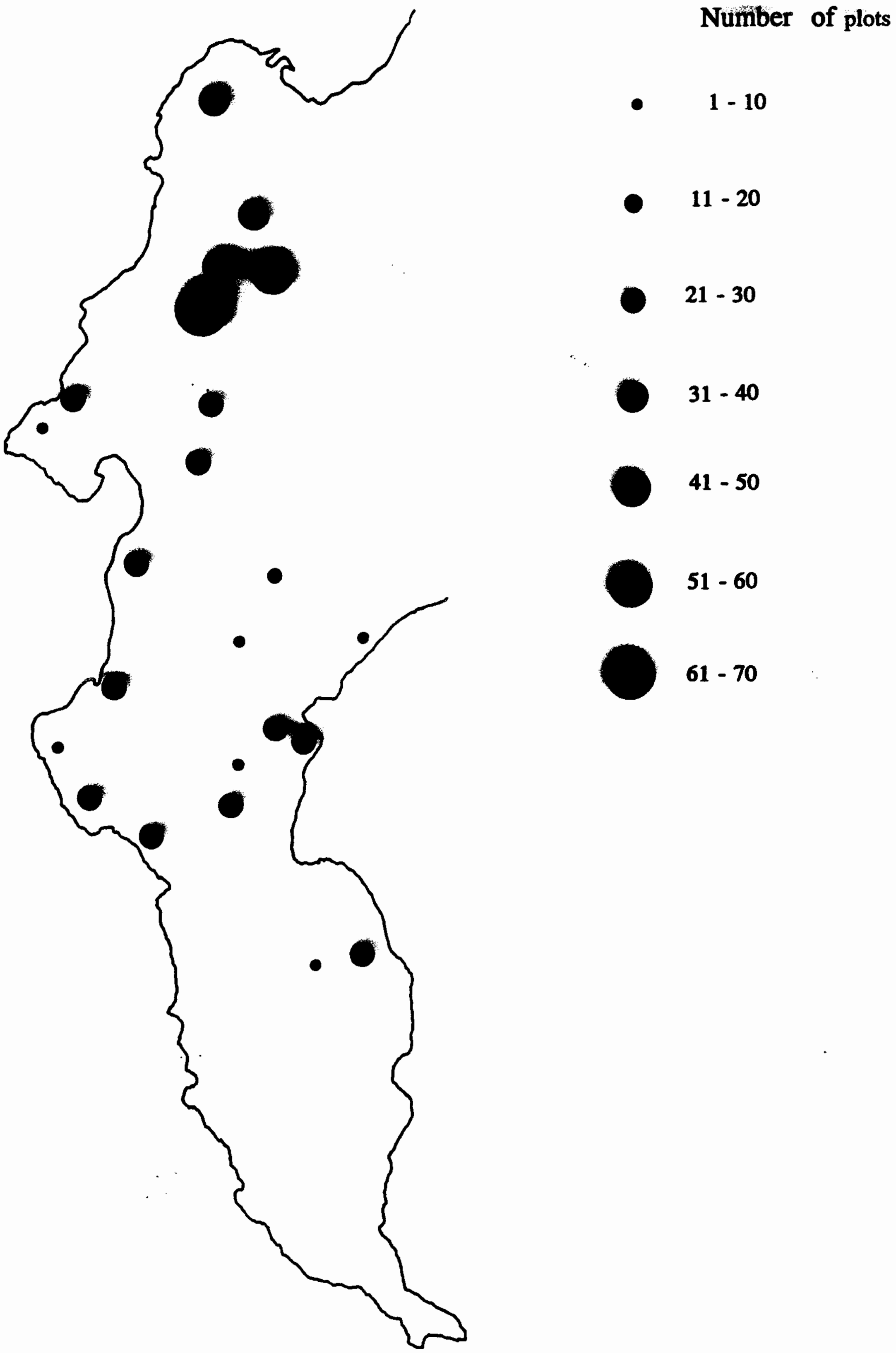
Rhus tomentosa

Salix hirsuta

Scutia myrtina

Secomone alpini

Virgilia oroboides


Number of plots
1 - 10
11 - 20
21 - 30
31 - 40
41 - 50
51 - 60
61 - 70

Appendix 2. Map of peninsula showing distribution of sites.